

Volume 31		Numbers 7–8		15 May 2011		ISSN 0278-4343	
		<b>CONTINENTAL SHELF RESEARCH</b>					
Editors: <b>Michael Collins</b> Southampton, UK <b>Richard W. Sternberg</b> Seattle, WA, USA							
<b>Research Papers</b>							
C.M. Alonso-Hernández, F. Conte, C. Mistic, M. Barsanti, M. Gómez-Batista, M. Díaz-Asencio, A. Covazzi-Harraguet and F.G. Pannacollulli	749	An overview of the Gulf of Batabanó (Cuba): Environmental features as revealed by surface sediment characterisation					
M. Yaremchuk and A. Sentchev	758	A combined EOF/variational approach for mapping radar-derived sea surface currents					
W. Gong and J. Shen	769	The response of salt intrusion to changes in river discharge and tidal mixing during the dry season in the Modaomen Estuary, China					
T.A. Kniskern, J.A. Warrick, K.L. Farnsworth, R.A. Wheatcroft and M.A. Goffi	789	Coherence of river and ocean conditions along the US West Coast during storms					
E.H. Shadwick, H. Thomas, Y. Gratton, D. Leong, S.A. Moore, T. Papakyriakou and A.E.F. Prowse	806	Export of Pacific carbon through the Arctic Archipelago to the North Atlantic					
K. Kombiadou and Y.N. Krestenitis	817	Simulating the fate of mechanically eroded masses in the Thermaikos Gulf					
E. Zetsche, B. Thornton, A.J. Midwood and U. Witte	832	Utilisation of different carbon sources in a shallow estuary identified through stable isotope techniques					
Rob.L. Evans and D. Lizarralde	841	The competing impacts of geology and groundwater on electrical resistivity around Wrightsville Beach, NC					
P. Petrušević, J. Bye, J. Luick and C.E.P. Teixeira	849	Summer sea surface temperature fronts and elevated chlorophyll-a in the entrance to Spencer Gulf, South Australia					
		<i>Continued on outside back cover</i>					
		<a href="http://www.elsevier.com/locate/csr">www.elsevier.com/locate/csr</a>					

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

## Continental Shelf Research

journal homepage: [www.elsevier.com/locate/csr](http://www.elsevier.com/locate/csr)

## Research papers

## Shoreline foraminiferal thanatacoenoses around five eastern Caribbean islands and their environmental and biogeographic implications

Brent Wilson<sup>a,\*</sup>, Jacqueline I. Wilson<sup>b</sup><sup>a</sup> Petroleum Geoscience Programme, Department of Chemical Engineering, University of the West Indies, St. Augustine, Trinidad, West Indies<sup>b</sup> Centre for Medical Sciences Education, Faculty of Medical Sciences, University of the West Indies, St. Augustine, Trinidad, West Indies

## ARTICLE INFO

## Article history:

Received 3 December 2010

Received in revised form

3 February 2011

Accepted 13 February 2011

Available online 21 February 2011

## Keywords:

*Amphistegina gibbosa*

St. John

USVI

Hurricanes

Guyana current

Organic matter enrichment

## ABSTRACT

Foraminiferal thanatacoenoses were examined around five islands in the Caribbean Sea, which forms a single biogeographic province with respect to nearshore (< 3 m water depth) foraminifera, which live primarily on marine vegetation. On death, they become incorporated into the sediment. The assemblage at a site reflects the live assemblage and post mortem affects such as dissolution and transport during storms. Reefal species (*Amphistegina gibbosa*, *Asterigerina carinata*) are transported towards shore during storms. Foraminiferal thanatacoenoses were examined in 65 nearshore sediment samples from around five eastern Caribbean islands: St. John (US Virgin Islands), St. Kitts, Nevis, Bequia and Tobago. Cluster and principal components analyses distinguished the following environments (indicator species in parentheses):

1. Sediment associated with mangroves (*Ammonia sobrina*),
2. Bays subject to organic matter enrichment (*Quinqueloculina poeyana*, *Triloculina rotunda*, *T. trigonula*),
3. Areas subject to moderate sediment flux during storms (*Quinqueloculina auberiana*, *Nodobaculiella mexicana*, *Peneroplis proteus*, *Archaia angulatus*),
4. Locations subject to high sediment flux during storms (*Amphistegina gibbosa*),
5. Sites little stressed by organic matter enrichment or storms (*Discorbis rosea*).

The majority of samples were from sites in the last category. The data from this study could form the nucleus of a catalogue of Caribbean beaches and their environmental influences.

© 2011 Elsevier Ltd. All rights reserved.

## 1. Introduction

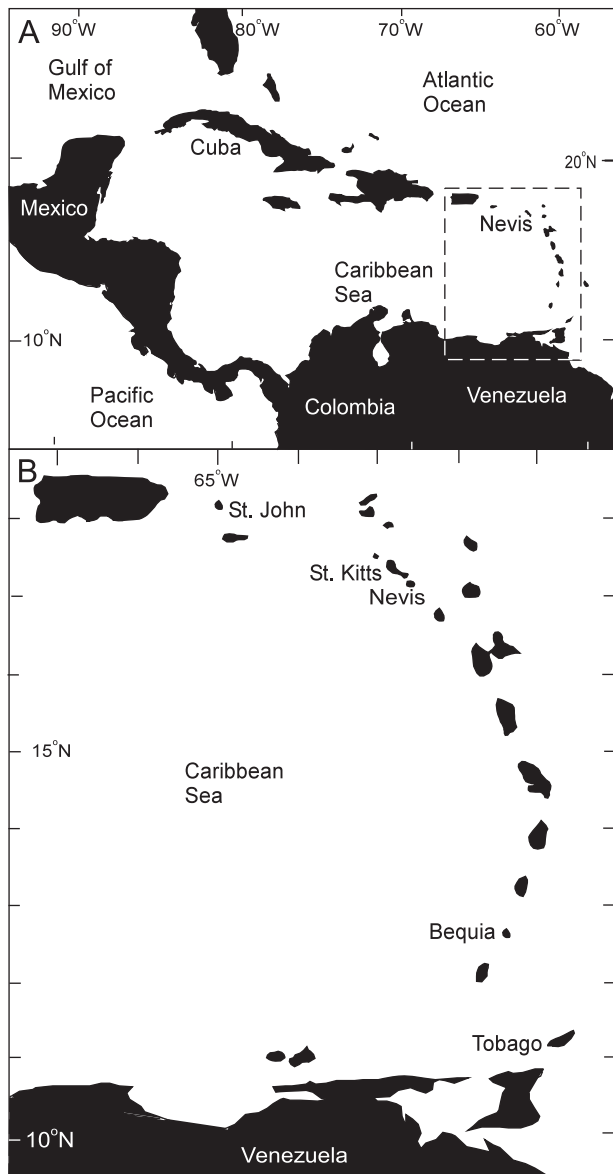
The Foraminifera is a class of small (usually < 1 mm) amoeboid protists with reticulating rhizopods that produce a chambered test (shell) that can be preserved after death. They construct their tests either by agglutinating sediment particles or secreting calcium carbonate, and abound in all marine environments. They are particularly diverse in tropical reefal environments (Murray, 2006) such as those in the Caribbean Sea, which is bordered to the north and east by islands that are encircled by coral reefs but separated by more or less deep water (Fig. 1). The nearshore (< 3 m water depth) benthonic foraminifera around these islands were first studied by d'Orbigny (1839) and have since been reported in > 100 papers (Culver and Buzas, 1982). Within these nearshore areas they live

primarily on marine vegetation (Cushman, 1922; Steinker and Clem, 1984). Although Martin and Wright (1988) concluded that much ecological information is lost when they die and their tests become incorporated into the sediment, much useful information remains. Thus, Seiglie (1971) was able to use sediment assemblages to detect pollution by organic matter in some Caribbean bays. Given that foraminiferal tests vary in shape and size and so react differently to hydrodynamic forces (Martin and Liddell, 1991), sediment assemblages have the potential to indicate which beaches on different islands are subject to organic pollution or similar hydrodynamic conditions. This has implications for land use planning.

Although the channels separating the islands of the eastern Caribbean potentially act as barriers to dispersal to nearshore organisms, Culver and Buzas (1982) concluded on the basis of species presence-absence that many foraminiferal species are ubiquitous within the region. However, the vectors of percentage abundances of species forming the thanatacoenoses within the sediment vary at smaller, intra-island scales. Brasier (1975) qualitatively discerned several distinct communities around

\* Corresponding author. Tel.: +1 868 662 2002x3676.

E-mail addresses: [brent.wilson@sta.uwi.edu](mailto:brent.wilson@sta.uwi.edu) (B. Wilson), [jacqui.wilson@sta.uwi.edu](mailto:jacqui.wilson@sta.uwi.edu) (J.I. Wilson).



**Fig. 1.** (A) The Caribbean Sea showing the location of the study area. (B) The eastern Caribbean Sea showing the locations of St. John, St. Kitts, Nevis, Bequia and Tobago.

Barbuda, including (a) a thin shelled miliolid-dominant assemblage is associated with backreef seagrass communities, (b) a miliolid-soritid-rotaliid-discorbid assemblage in interreef pockets, channels and sand blankets, and (c) an amphisteginid-miliolid-cassidulinid-textulariid-dominated assemblage associated with coral-algal rubble on the forereef talus slope. He distinguished a distinct shore zone around the entire island that he stated to range “from the water’s edge to 1 m depth” that he stated to be “characterized by thick-shelled forms washed in from nearshore areas”. A high percentage of the assemblage within the unstable shore zone sands was damaged.

Wilson (2006b, 2008) quantitatively examined the foraminiferal assemblages in twenty four samples from around Nevis (Fig. 2) and one from Sand Bank Bay, St. Kitts. All were from bare sediment in shore zone water mostly < 1 m deep. In contrast to Brasier’s (1975) suggestion that there is only a single shore-zone thanatacoensis around Barbuda, Wilson (2006b) used cluster analysis to group Nevis shore zone samples into six clusters. Most, however, contained few samples. Fifteen with abundant

*Discorbis rosea* were drawn from diverse locations around the island and grouped as a generalized cluster. This was interrupted at various places (especially along the north coast and in Cades Bay, a low energy site on the western coast) by smaller clusters. Thus, Wilson (2006b) found samples from the windward (eastern) and leeward (western) coasts to cluster together. The cluster along the northern coast contained abundant *Archaias angulatus* (Wilson, 2006a, Fig. 3) and *Amphistegina gibbosa*, the latter of which lives in reefal water (Baker et al., 2009). *Archaias angulatus* has been reported around Florida to live in the shallow backreef < 2 m deep (Martin, 1986; Souder et al., 2010). However, it apparently lives in deeper water around the Lesser Antilles; Wilson and Ramsook (2007) recorded only 47 *A. gibbosa* and six *A. angulatus* among 11,150 live foraminifera recovered from epiphytal communities in water < 1 m around Nevis. Cades Bay contained abundant *Ammonia sobrina*, *Quinqueloculina lamarckiana*, *Q. tricarinata*, *Q. poeyana*, *Rosalina floridana*, *Triloculina rotunda* and *T. trigonula*—an association concluded by Wilson and Ramsook (2007) to be indicative of organic matter enrichment.

With the exception of Culver and Buzas’s (1982) compilation, few studies have compared shore zone foraminiferal assemblages between the islands. d’Orbigny (1839) described many species from Cuba, Jamaica, Martinique, St. Thomas and Guadeloupe, among others. Hofker (1976) tabulated assemblages in samples collected in the 1950s through 1970s from many islands between the Cayman Islands (west) and Dominica (southeast). The localities he recorded included Turner and Frank Bays, St. John, US Virgin Islands and Frigate Bay, St. Kitts, which were sampled during this study. He reported abundant *Discorbis rosea* at Turner Bay contained, but did not record this species from either Frank or Frigate Bay. The sparse assemblage in Frigate Bay contained *Amphistegina radiata*, *Archaias angulatus*, *Massilina gualtieriana*, *Quinqueloculina quadrilatera* and *T. tricarinata* and *T. trigonula*. These data confirm that thanatacoenosis composition and structure varies both around and between islands.

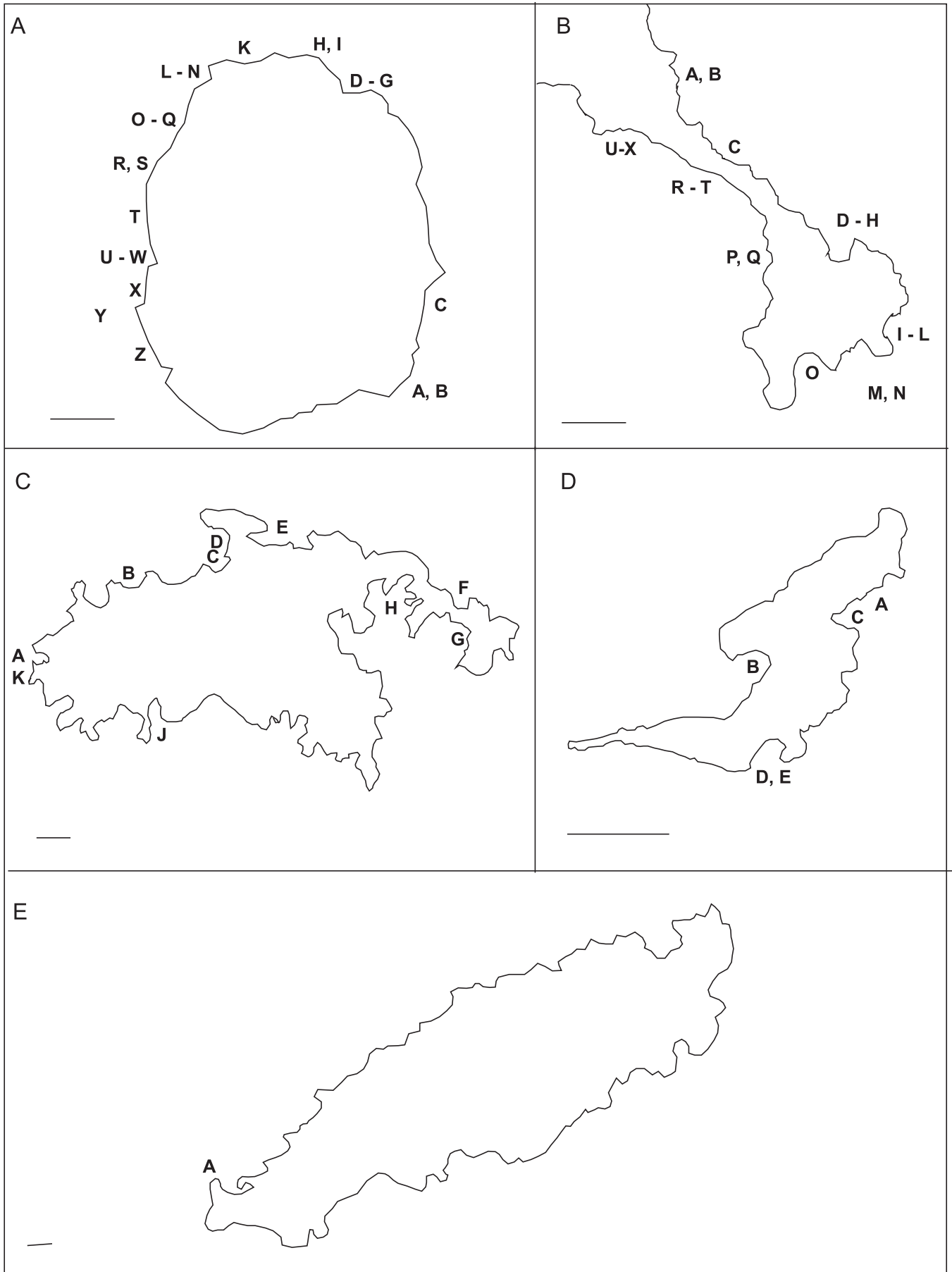
This study builds on previous work by examining shore zone foraminiferal thanatacoenoses around five islands in the eastern Caribbean Sea. Cluster analysis is used to determine which bays on the different islands contain comparable shore zone foraminiferal assemblages (although, the samples being collected over many years, it is not certain that they still do). Principal components analysis (PCA) is used to determine species’ associations. The biogeographic and land use implications of the findings are discussed.

## 2. Materials and methods

Sixty-six samples were obtained from five islands throughout the eastern Caribbean (Fig. 1, Table 1) by collecting the top 1 cm of sediment over an area of  $\geq 100$  cm<sup>2</sup>. From NW to SE, these are:

1. St. John, US Virgin Islands (18°21’N, 64°44’W), 11 samples collected in 1997, prefixed SJ,
2. St. Kitts, South East Peninsula only (17°20’N, 62°45’W), 24 samples prefixed SK,
3. Nevis (17°10’N, 62°35’W), 25 samples collected in 1990–1993, prefixed N; for details, see Wilson (2006a, b, Wilson, 2008),
4. Bequia St. Vincent and the Grenadines (13°15’N, 61°12’W), 5 samples collected 2006, prefixed B,
5. Tobago (11°11’N, 60°42’W), 1 sample collected 2010, prefixed T.

This is the first published study of foraminifera from Bequia. The South East Peninsula of St. Kitts was sampled in 1993 and 2006; sample numbers from the earlier occasion are distinguished in Table 1 with an asterisk. A sample from Coral Harbor, St. John (numbered SJ:I), yielded only twelve specimens (mostly



**Fig. 2.** The five islands studied, with sample locations. For names of locations, see Table 1. Scale bar in all cases 1 km long. North at top. (A) Nevis, samples prefixed N. (B) South East Peninsula, St. Kitts, samples prefixed SK. (C) St. John, samples prefixed SJ. (D) Bequia, samples prefixed B. (E) Tobago, sample prefixed T.

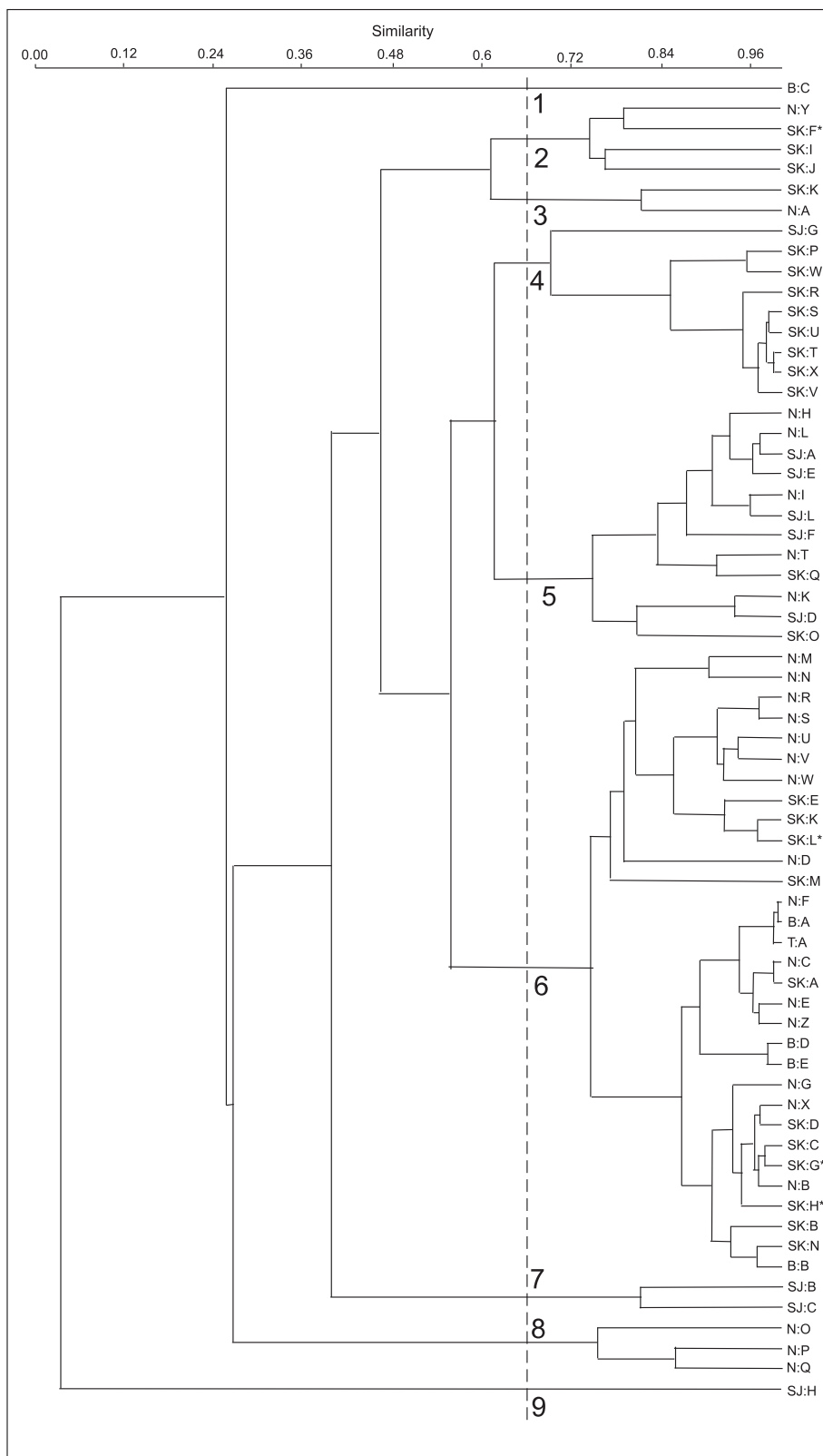


Fig. 3. Dendrogram of foraminiferal assemblages in 65 samples studied. For explanation of sample prefixes, see Section 2.

*Ammonia sobrina*) and is not considered further. Sample SJ:H (Princess Bay, St. John) differed from the others in comprising not sand but mud collected immediately adjacent a stand of the mangrove *Rhizophora mangle*. The remaining samples were taken from bare sand at  $\leq 3$  m (mostly  $\leq 1$  m) water depth. Where a

bay was vegetated, samples were taken from sand surrounding the seagrass meadow and from bare patches (white holes) within the meadow.

The samples were not stained to distinguish live foraminifera from dead. They were washed over a 63  $\mu$ m mesh to remove silt

**Table 1**

Sample abbreviations and locations. Samples from St. Kitts collected in 1993 are indicated with an asterisk. For years for other samples, see Section 2.

Nevis		St. John		St. Kitts	
Windward Beach	N:A	Cruz Bay	SJ:A	Half Moon Bay (West)	SK:A
Windward Beach	N:B	Trunk Bay	SJ:B	Half Moon Bay (West)	SK:B
Huggin's Bay	N:C	Maho Bay	SJ:C	North Friar's Bay	SK:C
Long Haul Bay	N:D	Francis Bay	SJ:D	Sand Bank Bay	SK:D
Long Haul Bay	N:E	Leinster Bay	SJ:E	Sand Bank Bay	SK:E
Long Haul Bay	N:F	Haulover Bay	SJ:F	Sand Bank Bay	SK:F*
Long Haul Bay	N:G	Hansen Bay	SJ:G	Sand Bank Bay	SK:G*
Nisbet Plantation	N:H	Princess Bay	SJ:H	Sand Bank Bay	SK:H*
Nisbet Plantation	N:I	Fish Bay	SJ:I	Turtle Beach	SK:I
Hurricane Cove	N:K	Frank Bay	SJ:L	Turtle Beach	SK:J
Mosquito Bay	N:L			Turtle Beach	SK:K
Mosquito Bay	N:M	<b>Bequia</b>		Turtle Beach	SK:L*
Mosquito Bay	N:N	Industry Bay	B:A	Cockleshell Bay	SK:M
Cades Bay	N:O	Admiralty Bay	B:B	Cockleshell Bay	SK:N
Cades Bay	N:P	Spring Bay	B:C	Major's Bay	SK:O
Cades Bay	N:Q	Friendship Bay	B:D	Whitehouse Bay	SK:P
Mariners' Bar	N:R	Friendship Bay	B:E	Whitehouse Bay	SK:Q
Mariners' Bar	N:S			South Friar's Bay	SK:R
Four Seasons Resort	N:T	<b>Tobago</b>		South Friar's Bay	SK:S
Rest Haven	N:U	Pigeon Point	T:A	South Friar's Bay	SK:T
Rest Haven	N:V			Frigate Bay Beach (SE)	SK:U
Rest Haven	N:W			Frigate Bay Beach (SE)	SK:V
Gallow's Bay	N:X			Frigate Bay Beach (NW)	SK:W
Offshore Gallow's Bay	N:Y			Frigate Bay Beach (NW)	SK:X
Bath Plain	N:Z				

and clay, and then dried over a gentle heat. As implied by the tables published by Hofker (1976), the proportion of sediment as foraminifera varies between beaches. Approximately equal amounts of sediment from each sample were picked clean of benthonic foraminifera. Thus, the number of specimens recovered varied from sample to sample. Species were identified using Cushman (1921, 1922, 1923, 1929, 1930, 1931), Brooks (1973), Hofker (1956, 1964, 1971, 1976, 1980), Todd and Low (1971) and Schnitker (1971), and the number of specimens per species per sample counted. The number of species picked from a sample (species richness  $S$ ) is a function the number of specimens picked (Buzas et al., 1977), so the diversity of the assemblage in each sample was assessed using not  $S$ , but the information function  $H$  ( $= -\sum p_i \cdot \ln p_i$ , where  $p_i$  is the proportional abundance of the  $i$ th species). The value of  $H$  is virtually independent of sample size (Hayek and Buzas, 2010).

Samples were grouped using Q-mode cluster analysis (paired group method) of species forming > 5% of the recovery from any one sample, clustering using the Morisita coefficient as this is insensitive to sample size (Hammer and Harper, 2005). R-mode (species-wise) PCA with varimax rotation was used to investigate associations between species. All calculations were performed using the freeware PAST of Hammer et al. (2001).

### 3. Results

A total of 20,424 benthonic foraminiferal tests in 172 species or species groups were picked from the samples (Supplementary information, Data Repository 1). However, most were rare, only 32 species and one group (miscellaneous *Triloculina* spp.) forming > 5% of the recovery from any one sample (see Appendix). All these species are robust (Martin and Wright, 1988) and preserve readily. Of these, the single most abundant species was *Disorbis rosea*, which formed 24.9% of the total recovery. The second most abundant species, *Archaias angulatus*, formed 10.8% of total recovery, while *Asterigerina carinata* and *Amphistegina gibbosa* formed 7.7% and 6.8%, respectively. Each of these 33 species/species groups was on average recorded from ~35 samples (standard deviation 17.2 samples). Five

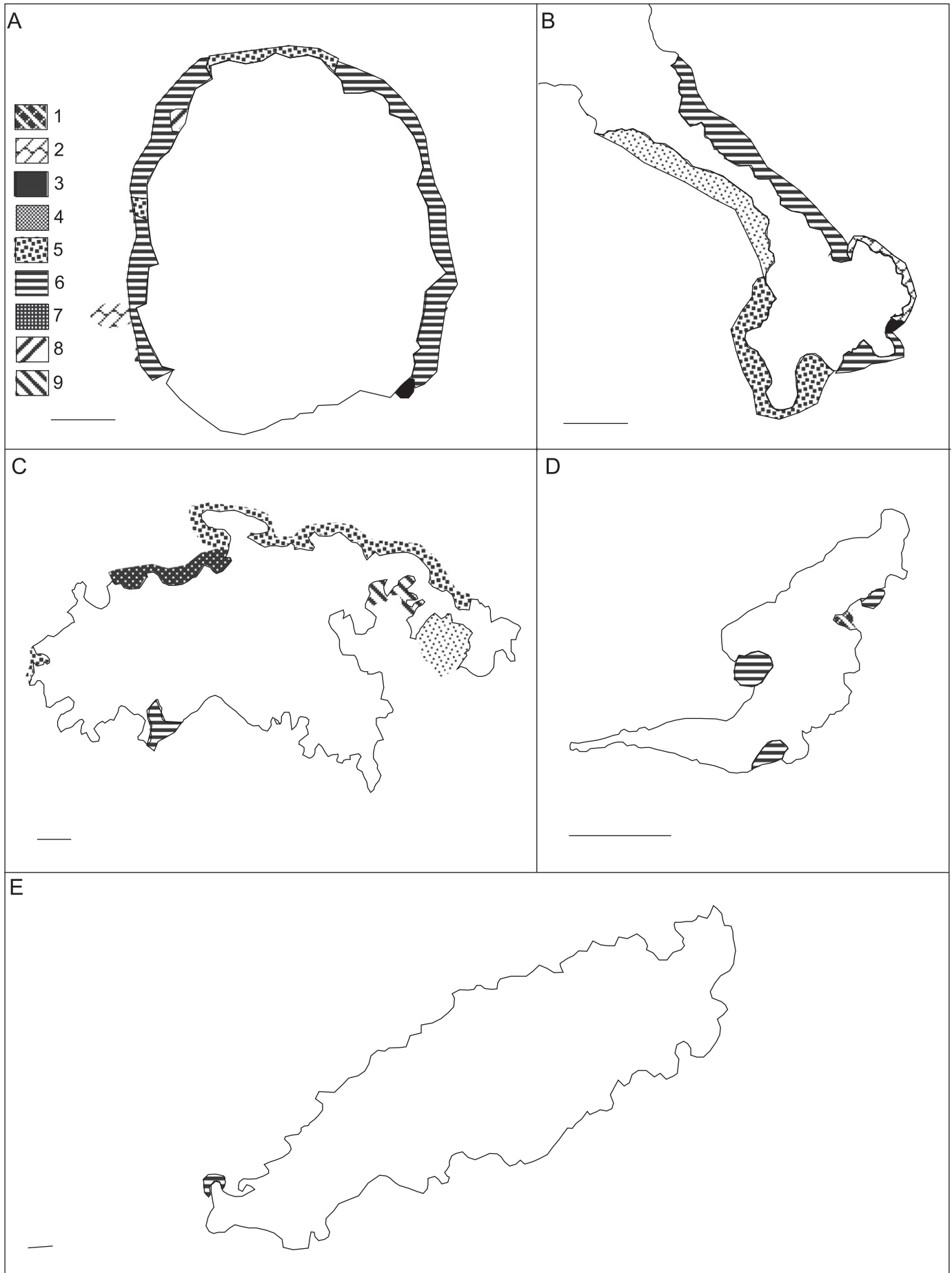
species were recorded from  $\geq 60$  samples: *A. gibbosa*, *A. angulatus*, *A. carinata*, *D. rosea* and *Peneroplis proteus*. The least widespread of these common species were *Cymbaloporetta atlantica* and *Massilina gualtieriana* (11 samples each), while the group *Triloculina* sp. was recorded from 9 samples.

Biodiversity measured using the information function ranged between  $H=0.623$  (T:A, Pigeon Point, Tobago) and 3.62 (N:P, Cades Bay, Nevis). The value of  $H$  was < 1.0 in three samples: T:A, Pigeon Point, Tobago; B:A, Industry Bay, Bequia; and SJ:H, Princess Bay, St. John. It was > 3.5 in three samples: N:P and N:Q (both from Cades Bay, Nevis) and SK:I (Turtle Beach, St. Kitts).

Q-mode cluster analysis revealed nine distinct clusters when the phenon line for the dendrogram was placed at a similarity of 0.65. The number of samples per cluster ranged from one (Clusters 1 and 9) to thirty-one (Cluster 6; Fig. 3). Clusters with one sample came from Spring Bay, Bequia (Cluster 1) and Princess Bay, St. John (Cluster 9), but these differed markedly. Cluster 1 was dominated by *Discorbis granulosa* and *D. auberii*, contained only 6.5% *D. rosea*, and had a high diversity ( $H=3.11$ ). Cluster 9 was dominated overwhelmingly by *Ammonia sobrina* and had a low diversity ( $H=0.993$ ).

Clusters 7 and 8 contained material from a single island (Fig. 4). Cluster 7 consisted of two samples from the adjacent Trunk and Maho Bays, NW St. John, which were remarkable for their high percentages (27% and 32.5%, respectively) of *Peneroplis carinatus* compared to other locations (the mean recovery of *P. carinatus* across all samples was 2.8%). Cluster 8 contained three samples from Cades Bay, Nevis, with high percentages of *Quinqueloculina poeyana*, *Triloculina rotunda* and *T. trigonula*, and low percentages of *D. rosea*.

The four clusters from a single island are small (one to three samples). Cluster 4, which is larger, contains eight samples from St. Kitts (South Friar's Beach and Frigate Bay) and one from St. John (Hansen Bay). *Peneroplis proteus* and *Quinqueloculina auberiana* form 12.7% and 21.3%, respectively, of the mean recovery from these (cf. the mean recovery per sample of both species across all 65 analysed samples was 4.5%). Cluster 5 contained 12 samples across St. Kitts, Nevis and St. John. Of these, three were recovered from the north coast of Nevis (N:H and N:I,



**Fig. 4.** The five islands studied showing the distributions of clusters. Key in figure A applies to all maps. (A) Nevis. (B) South East Peninsula, St. Kitts. (C) St. John. (D) Bequia. (E) Tobago, Scale bar in all cases 1 km long.

Nisbet Plantation: N:K, Hurricane Cove) and two came from its western, leeward coast (N:L, head of Mosquito Bay; N:T, at Four Seasons Resort). Five samples were from St. John (SJ:A, Cruz Bay; SJ:D, Francis Bay; SJ:E, Leinster Bay; SJ:F, Haulover Bay; SJ:L, Frank Bay) and two from St. Kitts (SK:O, Major's Bay; SK:Q, Whitehouse Bay). These 12 samples contained particularly high mean percentages of *Archaias angulatus* (mean 32.8%) and *Amphistegina gibbosa* (12.0%) but relatively low percentages of *D. rosea* (18.5%) and *Q. auberiana* (1.0%).

Thirty-one samples (48% of the 65 analysed) were placed in Cluster 6, which did not contain any samples from St. John. Fifteen were from the eastern and western coasts of Nevis and eleven from St. Kitts, where they came from the NE and SE coasts of the South East Peninsula (Half Moon Bay through Cockleshell Bay). This cluster contains a considerably greater than mean percentage of *D. rosea* (mean in Cluster 6, 41.0%) and a lower percentage of *A. angulatus* (mean 5.6%).

Principal components analysis was conducted on the 33 species/species groups forming >5% of the recovery from any one sample. Only the first two factors are considered here (Table 2). Factor 1 comprised 22.5% of the total variance, while Factor 2 accounted for 8.7%. *Quinqueloculina poeyana* had the highest loading on Factor 1 and *Discorbis rosea* the lowest. While *D. rosea* was recovered from all 65 samples analysed, *Q. poeyana* was recovered from only 23 and was generally rare (mean recovery 0.5% across all 65 samples). It formed >3% of recovery in samples from two sites only: Cades Bay, Nevis and Maho Bay, St. John. At these sites *D. rosea* formed <5.5% of the recovery per sample. On factor 2 *Quinqueloculina auberiana* had the highest loading and *A. gibbosa* the lowest. *Amphistegina gibbosa* was recovered from all but one sample (Princess Bay, St. John), and mean recovery per sample was 7.3%. Recovery of *A. gibbosa*

exceeded 15% in seven samples, of which four were from Nevis (N:C, Huggin's Bay, N:D, Long Haul Bay; N:H, Nisbet Plantation, N:K, Hurricane Cove), one from St. John (SJ:D, Francis Bay), one from St. Kitts (SK:B, Half Moon Bay [West]) and one from Bequia (B:B, Admiralty Bay). In contrast, *Q. auberiana* was recovered from 21 samples, but formed >10% of the recovery from ten samples only. Of these, one was on Nevis (N:R, Mariners' Bar), and the remainder on St. Kitts (Cockleshell Bay, South Friar's Bay and Frigate Bay).

#### 4. Discussion

Culver and Buzas (1982) examined the distributions of 1189 species of benthonic foraminifera at 338 Caribbean localities and found on the basis of presence/absence data that only 130 species occurred at  $\geq 13$  localities (i.e., only 11% of the species occurred at  $\geq 4\%$  of the localities). Nevertheless, they concluded that the vast majority of these 130 species "could be assigned to ubiquitous geographic and shallow shelf depth distributions."

For this study, species were termed 'common' when they comprised >5% of the recovery from any one of the 65 samples. Of the 172 species/species groups recorded, only 32 species and one group (19% of total species/species groups) fit this criterion. These were widespread across the islands, however, occurring in a mean of 35 samples (54% of samples analysed). At the island level, all 33 species/species groups were recorded from Nevis, all but *Cymbaloporetta atlantica*, *Massilina gualtieriana* and *Triloculina* spp. from St. John, all except *Triloculina* spp. from St. Kitts and all but the following seven species/species groups from Bequia: *Ammonia sobrina*, *M. gualtieriana*, *Nodobacularella mexicana*, *Quinqueloculina boschiana*, *Q. seminulum*, *Rosalina floridana* and *Triloculina* sp. Radford (1976, 1998) suggested that >300 species of benthonic foraminifera live around Tobago—although Murray (2006) suggested that she split some species too finely. Nevertheless, she recorded 19 of the 33 common species. These data do not contradict the contention by Culver and Buzas (1982) that the nearshore of the Caribbean Sea comprises a single biogeographic province with respect to benthonic foraminifera.

This study does not provide a snapshot of the eastern Caribbean at a single time, the samples having been collected over an extended period during which the foraminiferal thanatacoenosis at any site may have changed (cf. Hallock et al., 2003). However, the data provided for each island provide a baseline against which future samples may be compared. Furthermore, the islands fall into two groups with respect to sampling time (Nevis+St. John; St. Kitts+Bequia+Tobago) within which the islands can be compared directly. Whereas most samples from Nevis were from cluster six, only one sample from St. John came from this cluster. Most samples from St. John were from cluster 5. Most samples from St. Kitts, Bequia and Tobago likewise came from cluster six.

At the intra-island level, assemblages varied between samples. The thanatacoenosis preserved at a site is a function of (a) the composition of the live, predominantly epiphytal assemblage in the vicinity and (b) post mortem affects. The latter consists of loss through dissolution and abrasion (Martin and Liddell, 1991) and transport during storms. The eastern Caribbean lies within the Atlantic hurricane belt, the climate of which is characterised by pronounced wet and dry seasons. The former are marked by hurricanes and tropical storms, of which the NE Caribbean Sea was impacted by >60 between 1871 and 1986 alone (Lugo et al., 2000). Wilson (2010) found that hurricanes do not impact on the composition of the nearshore epiphytal fauna. Storms, however, winnow smaller foraminiferal tests from nearshore sediment and transport reefal (*Amphistegina gibbosa*, *Asterigerina carinata*)

**Table 2**

Factor loadings of species following principal components analysis with varimax rotation. Species with highest and lowest loadings on each factor in bold.

Species	Factor 1	Factor 2
<i>Ammonia sobrina</i>	0.073	-0.010
<i>Amphistegina gibbosa</i>	-0.238	<b>-0.391</b>
<i>Archaias angulatus</i>	-0.168	0.174
<i>Asterigerina carinata</i>	-0.064	0.268
<i>Borelis pulchra</i>	-0.151	-0.056
<i>Cymbaloporetta atlantica</i>	-0.001	0.011
<i>Cymbaloporetta squamosa</i>	0.019	-0.131
<i>Discorbis auberii</i>	0.105	-0.100
<i>Discorbis granulosa</i>	-0.063	-0.067
<i>Discorbis rosea</i>	<b>-0.319</b>	-0.370
<i>Elphidium discoidale</i>	0.311	0.322
<i>Elphidium poeyanum</i>	0.841	0.016
<i>Massilina gualtieriana</i>	-0.021	-0.241
<i>Nodobacularella mexicana</i>	-0.088	0.812
<i>Peneroplis carinatus</i>	-0.059	-0.050
<i>Peneroplis pertusus</i>	0.010	-0.266
<i>Peneroplis proteus</i>	-0.100	0.742
<i>Planorbulina mediterraneensis</i>	0.650	-0.040
<i>Quinqueloculina auberiana</i>	-0.150	<b>0.856</b>
<i>Quinqueloculina boschiana</i>	0.833	-0.065
<i>Quinqueloculina lamarckiana</i>	0.444	0.006
<i>Quinqueloculina poeyana</i>	<b>0.976</b>	-0.049
<i>Quinqueloculina polygona</i>	0.186	-0.137
<i>Quinqueloculina seminula</i>	0.862	-0.074
<i>Quinqueloculina tricarinata</i>	0.803	-0.084
<i>Quinqueloculina venezuelaensis</i>	0.252	0.018
<i>Rosalina floridana</i>	0.962	-0.017
<i>Siphonaperta bidentata</i>	-0.031	0.370
<i>Sorites orbiculus</i>	0.094	-0.165
<i>Textularia candeiana</i>	-0.098	-0.064
<i>Triloculina rotunda</i>	0.962	-0.033
<i>Triloculina</i> sp.	-0.024	-0.196
<i>Triloculina trigonula</i>	0.842	0.004



and deep back reef (*Archaias angulatus*) species towards shore (Li and Jones, 1997; Li et al., 1997, 1998).

Cluster analysis of sediment assemblages around the eastern Caribbean islands reflects both the local, live assemblage and post mortem effects:

1. Cluster 9 (one sample; Princess Bay, St. John) is dominated overwhelmingly by *Ammonia sobrina* and reflects the proximity of mangroves (Culver, 1990; Todd and Bronnimann, 1957; Wilson et al., 2008).
2. Cluster 5 (12 samples) contained the only three samples recovered from the north coast of Nevis and was characterised by high percentages of large allochthonous species (*A. angulatus*, *A. gibbosa*) but low percentages of smaller species (*D. rosea*, *Q. auberiana*). Wilson (2006a, b) concluded this to reflect shoreward transport of sediment and winnowing of smaller specimens from these sites during storms when water is funnelled between Nevis and nearby St. Kitts. He also concluded that material from this coast was transported into Mosquito Bay, NW Nevis, during storms to become concentrated at the head of the bay (sample N:L). Similar allochthonous material was recovered from Four Seasons Resort, Nevis (which might explain why the hotel at this site is regularly damaged by storm surges during hurricanes) and from Cruz, Francis, Leinster, Haulover and Frank Bays, St. John. Major's and Whitehouse Bays on St. Kitts contain the same allochthonous assemblage.
3. Cluster 8 consists of three samples from Cades Bay, Nevis. These have a high diversity as measured using the information function  $H$  and contain abundant *Quinqueloculina poeyana*, *Triloculina rotunda* and *T. trigonula* but few *D. rosea*. This reflects organic matter loading at this site (cf. Wilson and Ramscook, 2007). *Discorbis rosea* and *Q. poeyana* had high but antithetic loadings on the first factor from principal components analysis, indicating that *D. rosea* can be used to detect sites little stressed by organic matter. The presence of moderate (~3.4%) *Q. poeyana* at Maho Bay, St. John, suggests that this site is also subject to organic matter loading. Two other sites with > 1% *Q. poeyana* were identified: Mosquito Bay and Rest Haven, Nevis. *Triloculina rotunda* formed  $\leq 4.0\%$  of the recovery from sediment samples in Mosquito Bay. The live, epiphytally fauna in Mosquito Bay was reported by Wilson and Ramscook (2007), who found *T. rotunda* to comprise 13–30% of live, epiphytally fauna on *Halimeda opuntia* and *Penicillus capitatus* heads, and *Q. poeyana* to form 2.6% of the recovery. This live assemblage they ascribed to organic matter enrichment from a leaking septic tank. Following Hallock et al.'s (2003) assertion that, given sufficient time, a change in the epiphytally assemblage will be reflected in the sediment assemblage, it follows that the difference between the proportions of *T. rotunda* and *Q. poeyana* in Mosquito Bay indicates that the organic matter enrichment has not been going on long enough to be reflected in the sediment thanatacoensis. Alternatively, it is possible that the sediment thanatacoensis in Mosquito Bay is being diluted by material washed in from the north coast of Nevis during storms. High loadings for *Rosalina floridana* and *T. rotunda* on Factor 1 from PCA indicate that these also can be used to detect sites subject to an enhanced organic matter flux.
4. Cluster 4 (South Friar's and Frigate Bays, St. Kitts; Hansen Bay, St. John) contains greater than average percentages of the thick shelled *Q. auberiana*, *P. proteus* and *A. angulatus*, but low percentages of *A. gibbosa* and *D. rosea*. This may reflect an intermediate susceptibility to hurricanes impacts. The second factor from PCA had high but antithetic loadings for *A. gibbosa* and *Q. auberiana* and serves to differentiate beaches with highest and intermediate impacts by hurricanes (see Wilson, 2006b). High positive loadings for *Nodobacularella mexicana*

and *Peneroplis proteus* indicate that these too are indicative of beaches with an intermediate susceptibility to hurricanes impacts. That the variance explained by factor 1 (ascribed to organic matter loading; 22.5%) exceeds that of factor 2 (hurricane impact; 8.7%) suggests that not all ecological information is lost (cf. Martin and Wright, 1988) despite reworking of sediment during storms.

5. Cluster 6 contained the majority of samples, but lacked any from St. John. These contained a mean of 41.0% *D. rosea* but few *A. angulatus*. Wilson and Ramscook (2007) found the epiphytally fauna in the pristine Long Haul Bay, Nevis ( $\leq 1$  m), to comprise 44–54% *D. rosea*. Wilson (2008) concluded that the difference between the epiphytally and sediment percentage abundances of *D. rosea* reflects shoreward movement of *A. gibbosa* and *A. carinata* during storms. This suggests that Cluster 6 was recovered from sites at which the sediment thanatacoensis has as yet been little impacted by anthropogenically produced organic carbon.

These findings suggest that foraminiferal assemblages have a role to play in land use development decisions (cf. Scott et al., 2001). Assemblages with many allochthonous *A. angulatus* and *A. gibbosa* can be used to identify sites most susceptible to damage by the sea during storms and those with high proportions of *Q. auberiana* and *N. mexicana* to discern beaches with an intermediate susceptibility. *Quinqueloculina poeyana* and *T. rotunda* indicate locations susceptible to organic matter enrichment.

It is unclear how the Caribbean region in general and the Lesser Antillean islands in particular developed a uniform near-shore foraminiferal fauna. Live epiphytally foraminifera may be rafted on floating marine vegetation. However, such a means is unlikely to explain inter-island transport within the eastern Caribbean. Surface currents flow diagonally across the region from southeast to northwest, rather than along the north-south island chain. Araújo and Machado (2008) recorded many of the species listed in this paper on coral reefs off Brazil. It is possible that floating vegetation from there is being washed northwest by the Guyana Current along a broad front that impacts all the islands of the eastern Caribbean Sea. Shulman and Bermingham (1995) appealed to a Brazilian origin for planktonic larval stages to explain why some coral reef fishes throughout the Caribbean show the same mitochondrial DNA haplotypes. They concluded that gene flow among fish populations “has not been constrained by present-day ocean currents.” Alternatively, the islands may be seeded by free-floating foraminiferal zygotes rather than epiphytally adults. It has long been appreciated that planktonic juvenile stages of organisms can aid in wide dispersal (Scheltema, 1986). Ávila et al. (2009) appealed to such a mechanism to explain how the molluscan fauna of the Azores was sourced from eastern North America. Alve and Goldstein (2003) found that foraminifera produce propagules < 63  $\mu\text{m}$  across, and it is possible that the Lesser Antilles are seeded by floating propagules washed northwards on the Guyana Current. Finally, migrating animals may also play a role. Foraminifera might be transported on the legs of itinerant birds, and Debenay et al., in press reported that foraminifera can pass unharmed through the guts of herbivorous, reef-dwelling fishes and concluded that this can have “a significant effect on their dispersion.” It is unclear, however, whether such fishes migrate as adults between the islands of the Caribbean.

## 5. Conclusions

The eastern Caribbean Sea comprises a single biogeographic province with respect to shore zone, epiphytally benthonic

foraminifera. That the same species are found around the different islands, but that different species have different ecological niches and hydrodynamic properties, makes the thanatacoenosis useful for identifying nearshore areas throughout the region subject to the same environmental influences. Statistical analyses of foraminiferal assemblages in sediment around five islands distinguished the following (indicator species in parentheses):

1. Sediment associated with a *Rhizophora* mangle (*Ammonia sobrina*),
2. Bays subject to organic matter enrichment (*Quinqueloculina poeyana*, *Triloculina rotunda*, *T. trigonula*),
3. Sites little stressed by organic matter enrichment (*Discorbis rosea*)
4. Bays subject to moderate sediment flux during storms (*Quinqueloculina auberiana*, *Nodobacularella mexicana*, *Peneroplis proteus*, *Archaias angulatus*),
5. Bays subject to high sediment flux during storms (*Amphistegina gibbosa*).

The results presented here have implications for land use planning. For example, as stated by Wilson (2006a, b), low energy sites on the western coast of Nevis could act as sinks for pollutants and so should be developed with care. Hallock et al. (2003) have shown that foraminiferal thanatacoenoses respond to anthropogenic and other environmental perturbations, albeit more slowly than biocoenoses. The data presented here form a useful baseline for the particular islands covered, in the case of Nevis extending back ~20 years. Resampling will reveal the impact of global and local development on nearshore thanatacoenoses. The data from this study could form the nucleus of a catalogue of Caribbean beaches and their environmental influences.

## Acknowledgements

Over the years we were assisted in the field by the late Robert Young and David Rollinson. The late Ed Towle of the Island Resources Foundation kindly provided funds for sample collection from St. John. A contribution from the Research and Publications Fund of the University of the West Indies is gratefully acknowledged.

## Appendix A. Species forming > 5% of the recovery from any one sample

*Ammonia sobrina* (Shupack)=*Rotalia beccarii* (Linné) var. *sobrina* Shupack, 1934  
*Amphistegina gibbosa* d'Orbigny, 1839  
*Archaias angulatus* (Fichtel and Moll)=*Nautilus angulatus* Fichtel and Moll, 1798  
*Asterigerina carinata* d'Orbigny, 1839  
*Borelis pulchra* d'Orbigny=*Alveolinella pulchra* d'Orbigny, 1839  
*Cymbaloporetta atlantica* (Cushman)=*Tretomphalus atlantica* Cushman, 1934  
*Cymbaloporetta squamosa* (d'Orbigny)=*Rotalia squamosa* d'Orbigny, 1826  
*Discorbis auberii* (d'Orbigny)=*Rosalina auberii* d'Orbigny, 1839  
*Discorbis granulosa* (Heron-Allen and Earland)=*Discorbina valvulata* (d'Orbigny) var. *granulosa* Heron-Allen and Earland, 1915  
*Discorbis rosea* (d'Orbigny)=*Rosalina rosea* d'Orbigny, 1839  
*Elphidium discoidale* (d'Orbigny)=*Polystomella discoidalis* d'Orbigny, 1839  
*Elphidium poeyanum* (d'Orbigny)=*Polystomella poeyana* d'Orbigny, 1839  
*Massilia gualtieriana* (d'Orbigny)=*Quinqueloculina gualtieriana* d'Orbigny, 1839

*Nodobacularella mexicana* (Cushman)=*Articulina mexicana* Cushman, 1922  
*Peneroplis carinatus* d'Orbigny, 1839  
*Peneroplis pertusus* (Forskål)=*Nautilus pertusus* Forskål, 1775  
*Peneroplis proteus* d'Orbigny, 1839  
*Planorbulina mediterraneensis* d'Orbigny, 1826  
*Quinqueloculina auberiana* d'Orbigny, 1839  
*Quinqueloculina bosciensis* d'Orbigny, 1839  
*Quinqueloculina lamarckiana* d'Orbigny, 1839  
*Quinqueloculina poeyana* d'Orbigny, 1839  
*Quinqueloculina polygona* d'Orbigny, 1839  
*Quinqueloculina seminulum* (Linné)=*Serpula seminulum* Linné, 1797  
*Quinqueloculina tricarinata* d'Orbigny, 1839  
*Quinqueloculina venezuelaensis* Bermudez and Selié, 1963  
*Rosalina floridana* (Cushman)=*Discorbis floridana* Cushman, 1922  
*Siphonaperta bidentata* (d'Orbigny)=*Quinqueloculina bidentata* d'Orbigny, 1839  
*Sorites orbiculus* (Forskål)=*Nautilus orbiculus* Forskål, 1775  
*Textularia candeiana* d'Orbigny, 1839  
*Triloculina rotunda* d'Orbigny, 1839  
*Triloculina* spp.  
*Triloculina trigonula* d'Orbigny, 1839

## Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.csr.2011.02.010.

## References

- Alve, E., Goldstein, S.T., 2003. Propagule transport as a key method of dispersal in benthic foraminifera (Protista). *Limnology and Oceanography* 48, 2163–2170.
- Araújo, T.M.F., Machado, A.J., 2008. Foraminíferos da superfície do talude continental superior do norte da Bahia, Brasil. *Revista de Geologia* 21, 49–77.
- Ávila, S.P., Marques da Silva, C., Schiebel, R., Cecca, F., Backeljau, T., De Frias Martins, A.M., 2009. How did they get here? The biogeography of the marine molluscs of the Azores. *Bulletin de la Societe Geologique de France* 180, 295–307.
- Baker, R.D., Hallock, P., Moses, E.F., Williams, D.E., Ramirez, A., 2009. Larger foraminifers of the Florida reef tract, USA: distribution patterns on reef rubble habitats. *Journal of Foraminiferal Research* 39, 267–277.
- Brasier, M.D., 1975. The ecology and distribution of recent foraminifera from the reefs and shoals around Barbuda, West Indies. *Journal of Foraminiferal Research* 5, 193–210.
- Brooks, W.W., 1973. Distribution of recent foraminifera from the southern coast of Puerto Rico. *Micropaleontology* 19, 385–416.
- Buzas, M.A., Smith, R.K., Beem, K.A., 1977. Ecology and systematics of foraminifera in two *Thalassia* habitats, Jamaica, West Indies. *Smithsonian Contributions to Paleobiology* 31, 1–139.
- Culver, S.J., 1990. Benthic foraminifera of Puerto Rican mangrove–lagoon systems: potential for paleoenvironmental interpretations. *Palaos* 5, 34–51.
- Culver, S.J., Buzas, M.A., 1982. Distribution of recent benthic foraminifera in the Caribbean region. *Smithsonian Contributions to Marine Science* 14, 1–382.
- Cushman, J.A., 1921. Foraminifera from the north coast of Jamaica. *Proceedings of the U. S. National Museum* 59, 47–82.
- Cushman, J.A., 1922. Shallow-water foraminifera of the Tortugas region, 17. *Carnegie Institution of Washington* 3–85.
- Cushman, J.A., 1923. The foraminifera of the Atlantic Ocean, part 4: Lagenidae. *United States National Museum Bulletin* 104 (4), 1–228.
- Cushman, J.A., 1929. The foraminifera of the Atlantic Ocean, part 6: Miliolidae. *United States National Museum Bulletin* 104 (6), 1–129.
- Cushman, J.A., 1930. The foraminifera of the Atlantic Ocean, part 7: Nonionidae, Camerinidae, Peneroplidae and Alveolinellidae. *United States National Museum Bulletin* 104 (7), 1–179.
- Cushman, J.A., 1931. The foraminifera of the Atlantic Ocean, part 8: Rotaliidae, Amphisteginidae, Calcarinidae, Cymbalopoertidae, Globorotalidae, Anomaliniidae, Planorbulinidae, Rupertiidae, and Homotremidae. *United States National Museum Bulletin* 104 (8), 1–179.
- d'Orbigny, A., 1839. Foraminifères. In: de La Sagra, R. (Ed.), *Histoire physique, politique et naturelle de l'île de Cuba* Arthur Bertrand, pp. 1–224.

- Debenay, J.-P., Sigura, A., Justine, J.-L. Foraminifera in the diet of coral reef fish from the lagoon of New Caledonia: predation, digestion, dispersion. *Revue de micropaléontologie*, in press, doi:10.1016/j.revmic.2010.04.001.
- Hallock, P., Lidz, B., Cockey-Burkhard, E.M., Donnelly, K.B., 2003. Foraminifera as bioindicators in coral reef assessment and monitoring: the FORAM index. *Environmental Monitoring and Assessment* 81, 221–238.
- Hammer, Ø., Harper, D.A.T., 2005. *Paleontological Data Analysis*. Wiley-Blackwell Oxford, UK 368 p.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* pp. <[http://palaeo-electronica.org/2001\\_2001/past/issue2001\\_2001.htm](http://palaeo-electronica.org/2001_2001/past/issue2001_2001.htm)>.
- Hayek, L.-A.C., Buzas, M.A., 2010. *Surveying Natural Populations: Quantitative Tools for Assessing Biodiversity*, 2nd ed. Columbia University Press, New York, USA 590 p.
- Hofker, J., 1956. Foraminifera Dentata: Foraminifera of Santa Cruz and Thatch Island, Virginia Archipelago, West Indies. *Spolia zoologica Musei Hauniensis* 15, 1–237.
- Hofker, J., 1964. Foraminifera from the tidal zone in the Netherlands Antilles and other West Indian islands. *Studies on the Fauna of Curacao and other Caribbean Islands* 21, 1–119.
- Hofker, J., 1971. The foraminifera of Piscadera Bay, Curacao. *Studies on the Fauna of Curacao and other Caribbean Islands* 35, 1–94.
- Hofker, J., 1976. Further studies on Caribbean Foraminifera. *Studies on the Fauna of Curacao and other Caribbean Islands* 40, 1–252.
- Hofker, J., 1980. The Foraminifera of the Saba Bank Expedition 1972 (Cigar Cruises 34, 35). *Zoologische Verhandelingen Uitgegeven door het Rijksmuseum van Natuurlijke Historie te Leiden* 177, 73.
- Li, C., Jones, B., 1997. Comparison of foraminiferal assemblages in sediments on the windward and leeward shelves of Grand Cayman, British West Indies. *Palaios* 12, 12–26.
- Li, C., Jones, B., Blanchon, P., 1997. Lagoon-shelf sediment exchange by storms—evidence from foraminiferal assemblages, east coast of Grand Cayman, British West Indies. *Journal of Sedimentary Research* 67, 17–25.
- Li, C., Jones, B., Kalbfleisch, W.B.C., 1998. Carbonate sediment transport pathways based on foraminifera: case study from Frank Sound, Grand Cayman, British West Indies. *Sedimentology* 45, 109–120.
- Lugo, A.E., Rogers, C.S., Nixon, S.W., 2000. Hurricanes, coral reefs and rainforests: resistance, ruin and recovery in the Caribbean. *Ambio* 29, 106–114.
- Martin, R.E., 1986. Habitat and distribution of the foraminifer *Archaias angulatus* (Fichtel and Moll) (Miliolina, Soritidae), northern Florida Keys. *Journal of Foraminiferal Research* 16, 201–206.
- Martin, R.E., Liddell, W.D., 1991. In: Donovan, S.K. (Ed.), *Taphonomy of foraminifera in modern carbonate environments: implications for the formation of foraminiferal assemblages*. The Processes of Fossilization Belhaven Press, London, pp. 170–193.
- Martin, R.E., Wright, R.C., 1988. Information loss in the transition from life to death assemblages of foraminifera in back-reef environments, Key Largo, Florida. *Journal of Paleontology* 62, 399–410.
- Murray, J.W., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge, UK 438 p.
- Radford, S.S., 1976. Recent foraminifera from Tobago Island, West Indies. *Revista Espanola de Micropaleontología* 8, 193–218.
- Radford, S.S., 1998. Foraminifera from the Southern Caribbean-Atlantic Province. In: Ali, W., Paul, A., Young On, V. (Eds.), *Proceedings of the Third Geological Conference of the Geological Society of Trinidad and Tobago and the 14th Caribbean Geological Conference*, Port-of-Spain, Trinidad, pp. 163–178.
- Scheltema, R.S., 1986. Long-distance dispersal by planktonic larvae of shoal-water benthic invertebrates among central Pacific islands. *Bulletin of Marine Science* 39, 241–256.
- Schnitker, D., 1971. Distribution of foraminifera on the North Carolina continental shelf. *Tulane Studies in Geology and Paleontology* 8, 169–215.
- Scott, D.B., Mediolli, F.S., Schafer, C.T., 2001. *Monitoring of Coastal environments using Foraminifera and Thecamoebian indicators*. Cambridge University Press, Cambridge, UK 192 p.
- Seiglie, G.A., 1971. A preliminary note on the relationships between foraminifers and pollution in two Puerto Rican bays. *Caribbean Journal of Science* 11, 93–98.
- Shulman, M.J., Bermingham, E., 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* 49, 897–910.
- Souder, H.C., McCloskey, B., Hallock, P., Byrne, R., 2010. Shell anomalies observed in a population of *Archaias angulatus* (Foraminifera) from the Florida Keys (USA) sampled in 1982–83 and 2006–07. *Marine Micropaleontology* 77, 71–81.
- Steinker, D.C., Clem, K.V., 1984. Some nearshore foraminiferal assemblages from phytal substrates and bottom sediments, Bermuda. *The Compass* 61, 98–115.
- Todd, R., Bronnimann, P., 1957. Recent Foraminifera and Thecamoebina from the Eastern Gulf of Paria. *Cushman Foundation for Foraminiferal Research, Special Publication* 3, pp. 1–43.
- Todd, R., Low, D., 1971. Foraminifera from the Bahama Bank west of Andros Island. *US Geological Survey Professional Paper* 683-C, pp. 1–22.
- Wilson, B., 2006a. The environmental significance of *Archaias angulatus* (Miliolida, Foraminifera) in sediments around Nevis, West Indies. *Caribbean Journal of Science* 42, 20–23.
- Wilson, B., 2006b. The environmental significance of some microscopic organisms around Nevis, West Indies. *West Indian Journal of Engineering* 28, 53–64.
- Wilson, B., 2008. Population structures among epiphytal foraminiferal communities, Nevis, West Indies. *Journal of Micropaleontology* 27, 63–73.
- Wilson, B., 2010. Effect of hurricanes on guilds of nearshore epiphytal foraminifera, Nevis, West Indies. *Journal of Foraminiferal Research* 40, 327–343.
- Wilson, B., Miller, K., Thomas, A.-L., Cooke, N., Ramsingh, R., 2008. Foraminifera in the Mangal at the Caroni Swamp, Trinidad: diversity, population structure and relation to sea level. *Journal of Foraminiferal Research* 38, 127–136.
- Wilson, B., Ramsook, A., 2007. Population densities and diversities of epiphytal foraminifera on nearshore substrates, Nevis, West Indies. *Journal of Foraminiferal Research* 37, 213–222.